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Vertical and temporal distribution of the dinoflagellates *Dinophysis acuminata* and *D. norvegica* in the Baltic Sea

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We investigated the distributions of the toxic dinoflagellates *Dinophysis acuminata* and *D. norvegica* in the brackish Baltic Sea, and found them to differ both regarding their seasonality and their vertical distribution. *Dinophysis acuminata* was considerably more abundant, especially in the Gulf of Finland, where we observed an August peak of 14 300 cells l^{-1}. It occurred in elevated abundances during or after periods of high phytoplankton biomass in early and late summer. *Dinophysis norvegica* was abundant during a shorter period, peaking one month after the first *D. acuminata* maximum. While *D. norvegica* probably is restricted by both salinity and temperature in the northern Baltic Sea, the more tolerant *D. acuminata* thrives. The results presented here expand the wide range of scenarios in which *D. acuminata* may bloom worldwide. Both species mainly formed population maxima either in the mixed surface waters or near the thermocline. *Dinophysis acuminata* usually occurred in the illuminated and nutrient-poor mixed surface layer, but in the presence of light and a nutricline it formed distinct subsurface peaks. *Dinophysis norvegica* was not as sensitive to darkness and predominantly formed subsurface peaks, even below the euphotic zone. These occurrences were promoted by shallow stratification, and the combination of a deep mixed layer and cool surface waters drew the *D. norvegica* population closer to the surface. When *D. acuminata* and *D. norvegica* co-occurred, their abundances peaked at different depths; this was observed even when both species formed maxima in the surface layer.

Introduction

The dinoflagellates *Dinophysis acuminata* and *D. norvegica* have been recorded from all Baltic Sea subareas (Hällfors 2004) and are dominant among *Dinophysis* species in the northern Baltic Sea (Hajdu 2002). Particularly during the summer months, they regularly occur in abundances exceeding those that cause diarrhoetic shellfish poisoning (DSP) elsewhere (e.g. Hajdu 2002). Since cultivation of shellfish is restricted to the Kattegat region in the Baltic Sea, *Dinophysis* toxicity has until fairly recently received little attention in the northern sea areas. Here, DSP toxins have been found in water samples containing *Dinophysis* species, as well as in copepod

faecal pellets (Kuuppo *et al*. 2006), copepods (Setälä *et al*. 2009), blue mussels (Pimiä *et al*. 1997), and flounder (Sipiä *et al*. 2000), a fish species that feeds on blue mussels. Thus, although not constituting an acute threat to human health in the northern Baltic Sea, *Dinophysis* toxins are a potential risk for high-trophic-level consumers through bioaccumulation in the food web (cf. Kuuppo *et al*. 2006, Setälä *et al*. 2009).

Being flagellated and therefore motile, dinoflagellates have the potential to regulate their position in the water column, and both *D. acuminata* and *D. norvegica* often form distinct abundance peaks (e.g. Carpenter *et al*. 1995, Reguera *et al*. 2003, Lindahl *et al*. 2007). The stimuli and mechanisms regulating the vertical distributions of *Dinophysis* species are still not fully understood, since observations regarding these organisms are often ambiguous and inconsistent (e.g. Carvalho *et al*. 2008 and references therein). To complicate matters further, co-occurring *Dinophysis* species sometimes favour different depths (e.g. Hajdu 2002, Lindahl *et al*. 2007). Thus, no easy answers are to be expected if several species are addressed together as *Dinophysis* spp., or if co-occurring *Dinophysis* species are investigated one at a time, or if the vertical resolution of sampling is low. The general hypothesis that *Dinophysis* species favour a particular layer due to the availability of dissolved nutrients and/or food organisms has neither been challenged nor supported by *in situ* observations (Maestrini 1998). This still holds true a decade later, but it seems safe to assume that nutrition is a primary factor. Current knowledge suggests that an additional important nutritional incentive may be the distribution of prey organisms that are suitable as chloroplast sources. Such from other organisms through ingestion acquired plastids, called kleptochloroplasts, have been suggested for *Dinophysis* species (e.g. Janson 2004 and references therein), including *D. norvegica* (Minnhagen *et al*. 2008) and *D. acuminata* (Park *et al*. 2006), although recent studies on the latter species yielded differing results (Garcia-Cuetos *et al*. 2010).

Since *D. acuminata* has only recently been cultured successfully (Park *et al*. 2006), and *D. norvegica* not at all, observations of natural populations are still essential to further our understanding of their ecology, particularly their tendency to accumulate at certain depths. In the Baltic Sea, the vertical distribution of *Dinophysis* species has only been studied for short periods of time and/or at low vertical sampling resolution (Carpenter *et al*. 1995, Olli 1999, Gisselson *et al*. 2002, Setälä *et al*. 2005, Kuuppo *et al*. 2006, Hajdu *et al*. 2007). Moreover, *D. acuminata* and *D. norvegica* have rarely been investigated simultaneously.

Our hypothesis was that *D. acuminata* and *D. norvegica* favour different parts of the water column, which may be a consequence of different nutritional preferences. We furthermore wanted to determine whether the vertical distributions in the Baltic Sea are general, irrespective of sampling location or year. To do so, we used a high vertical sampling resolution to investigate the vertical and temporal distribution of *D. acuminata* and *D. norvegica* during three different summers and at several locations in the northern Baltic Sea.

Material and methods

Study area

The Baltic Sea (Fig. 1) is a semienclosed nontidal brackish water estuary with wide horizontal, vertical and seasonal variations in its physical and chemical characteristics (e.g. Voipio 1981, Wulff *et al*. 2001). The maximum depth is 459 m (mean depths of the Baltic proper and the Gulf of Finland are 67 m and 38 m, respectively), and a permanent halocline resides at 40–80 m depth (Mälkki and Tamsalu 1985, Alenius and Haapala 1992). The water column above the permanent halocline is stratified during summer and early autumn, with a seasonal thermocline typically situated between 10 and 30 m depth, separating the surface layer from cold deeper waters (Alenius and Haapala 1992) and effectively restricting the vertical transport of nutrients. There are high levels of dissolved organic humic substances in the Baltic Sea, the mean CDOM absorption being 1.94 m^{-1} and 1.20 m^{-1} in the western Gulf of Finland and northern Baltic proper, respectively (at wavelength 375 nm; P. Ylöstalo, J. Seppälä & S. Kai-

tala unpubl. data). Since these humic substances absorb solar radiation effectively, the euphotic zone is only some 15 m deep (Stigebrandt 2001).

Sampling

Three different datasets collected from open sea areas were utilised. In 1999 and 2000, sampling was performed at station BY31 (58°35´N, 18°14´E, depth 459 m, Fig. 1) in the western northern Baltic proper (henceforth WNBP). Samples for the *Dinophysis* abundance analysis were taken between 11:00 and 14:00 every other week from late June to mid-August in 1999 (every 2.5 m from the surface down to 25 m, on 22 June down to 20 m) and from May to September in 2000 (0, 2, 4, 6, 8, 10 m and every 2.5 m after that down to 25 m, before August also 1 m). In 2004, sampling was carried out once in May, weekly in June, twice in July and once in August at a total of three different locations. Samples were collected from 1, 3, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, and 20 m. In May, June and August, samples were taken between 9:30 and 13:00 at Längden (59°46´N, 23°16´E, depth 60 m, Fig. 1) in the western Gulf of Finland (henceforth WGF), in July at two locations in the eastern northern Baltic proper (henceforth ENBP) near the entrance to the Gulf of Finland (station ENBP1, 59°32´N, 22°50´E, depth 75 m; station ENBP2, 59°13´N, 22°19´E, depth 111 m, Fig. 1) between 10:00 and 11:00.

Samples for the nutrient analysis were taken at 5-m intervals from the surface down to 25 m in 1999 and 2000. In May 2004, nutrient data were provided by the Uusimaa Regional Environment Centre, which sampled the same location two days earlier, on 10 May. By calculating parametric Pearson's r (n = 8), we determined the correlations between the different sampling depths of 10 and 12 May to be 1 and 0.99 for salinity and temperature, respectively, indicating stable hydrography with no change in thermocline depth. The means were almost identical, which showed that the water mass properties were very similar on both occasions, i.e. no warming of water occurred. From the monitoring data provided by the Uusimaa Regional Environment Centre (four samplings in May 2004), we calculated that phosphate declined at the rate of ca. 0.003 μmol l^{-1} per day at the surface, while nitrite + nitrate was almost totally exhausted throughout the period, displaying no trend. Based on this, we consider the nutrient data of 10 May to be representative of the situation two days later, on 12 May. In June and July, nutrients were analysed from the same depths as the species analysis, in May and August from 1, 5, 10 and 20 m.

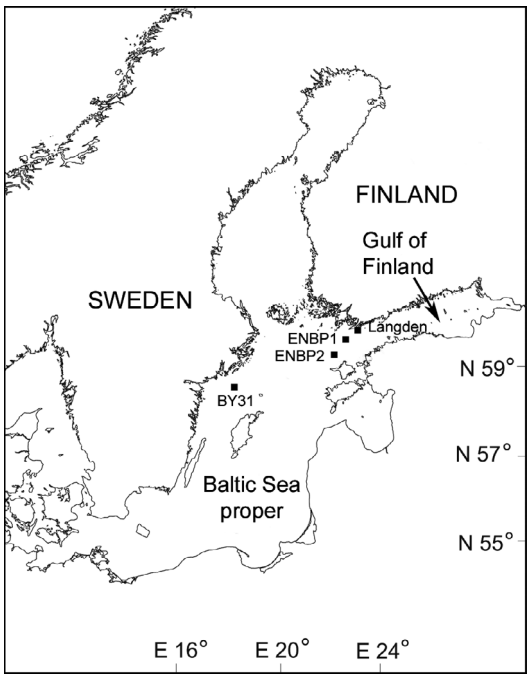

Fig. 1. Study area. The western northern Baltic proper (WNBP, station BY31) was sampled in 1999 and 2000, and the western Gulf of Finland (WGF, station Längden) and the eastern northern Baltic proper (ENBP, stations ENBP1 and ENBP2) were sampled in 2004.

Salinity (PSU) and temperature were measured with a CTD meter (SST, Meerestechnik Elektronik GmbH) in 1999 and 2000. In May and June 2004 an SIS CTDplus 100 (SiS Sensoren Instrumente Systeme GmbH), in July a SEABIRD SBE 911plus, and in August a SEACAT SBE 19-03 (both Sea-Bird Electronics, Inc.) CTD meter was used.

The depth of the euphotic zone, i.e. the depth to which 1% of the surface irradiation penetrates (Højerslev 1978) and below which phytoplankton cell respiration is considered to be greater

than photosynthesis, was calculated as twice the Secchi depth, in accordance with Niemi (1975), Højerslev (1978), and Aarup (2002).

Determination of nutrients

In 1999 and 2000, phosphate (PO_4) and dissolved inorganic nitrogen (DIN, i.e. ammonium NH_4, nitrite NO_2, and nitrate NO_3) were analysed using a Lachat QC 8000 analysator according to the QuikChem method by Lachat Instruments. The detection limits for PO_4, NH_4, NO_2, and NO_3 were 0.016, 0.04, 0.015, and 0.015 μmol l^{-1}, respectively.

In June 2004 nutrients were determined according to Koroleff (1976), using a Hitachi U-1100 spectrophotometer. In May and August PO_4 and NH_4 were measured manually, using a Shimadzu UV-1601 spectrophotometer. In May NO_2 + NO_3 was measured with a Bran+Lüebbe CFA AutoAnalyzer 3 and in August with a Lachat QC 8000 analysator and the QuikChem method by Lachat Instruments.

In July 2004 nutrients, with the exception of NH_4, were determined with the QuikChem method as above, while NH_4 was determined manually using the spectrophotometric method developed by Koroleff (1983) and using a PerkinElmer Lambda 2 UV/VIS spectrophotometer. In 2004 the detection limits for PO_4, NH_4, and NO_2 + NO_3 (NO_2 and NO_3 in July) were in the range of 0.05–0.06, 0.14–0.25, and 0.14–0.36 (0.06 and 0.10 in July) μmol l^{-1}, respectively.

All the above nutrient analyses are standardised and intercalibrated methods used in the laboratories of the University of Stockholm, the University of Helsinki, the Finnish Environment Institute (also responsible for analyses for the Uusimaa Regional Environment Centre) and the Finnish Institute of Marine Research, and the results are considered comparable.

Cell enumeration

All samples were preserved using acid Lugol's solution (Willén 1962) and sedimented in 50-ml chambers for at least 24 hours, following Utermöhl (1958). In 1999 and 2000, *Dinophysis* were counted from the entire chamber bottom using a Nikon Diaphot 114 inverted microscope with a 10× objective. In all, between 1 and 229 cells of each species were counted per sample, resulting in count-specific confidence limits (CL) between ±200% and ±13% (at 95% significance level; *see* Venrick 1978, Andersen and Throndsen 2003: 111–113). This means that the more cells were counted, the more reliable the results are. In 2004, a Leitz DM IRB inverted microscope with a 10× objective was used to analyse 60–79 random fields of view per chamber. Two parallel sedimentations and counts were performed from each sample for each species, except when ≥ 200 cells (CL ±14%) of a species were found in the first chamber. 1–207 cells per species were found per parallel, resulting in count-specific CLs between ±200% and ±14%. The variation in cell numbers between the two parallels was always within the expected limits (i.e. CL, cf. Andersen and Throndsen 2003).

Integrated total abundances of *D. acuminata* and *D. norvegica* were calculated for the 0–20 m layer (trapezoid integration). Normally, the cell numbers at 20 m were very low and the organisms present in deeper layers were assumed to represent a minor fraction of the population.

During the study period, several methods and apparatuses were used for the different measurements and analyses. All the institutes involved regularly participate in the intercalibration of methods within the framework of HELCOM monitoring and the QUASIMEME intercalibration (Quality Assurance of Information for Marine Environmental Monitoring in Europe); thus the results are considered comparable.

Results

Physicochemical parameters

During the study period, salinity varied between 5.5 and 6.9 in the top 20–25 m, and the temporal within-site variation was as great as the variation between sites. The density profile followed that of salinity closely, and both displayed at best only a slight increase with depth (data not shown). Likewise, the within-site variation in the euphotic zone depth was similar to that between

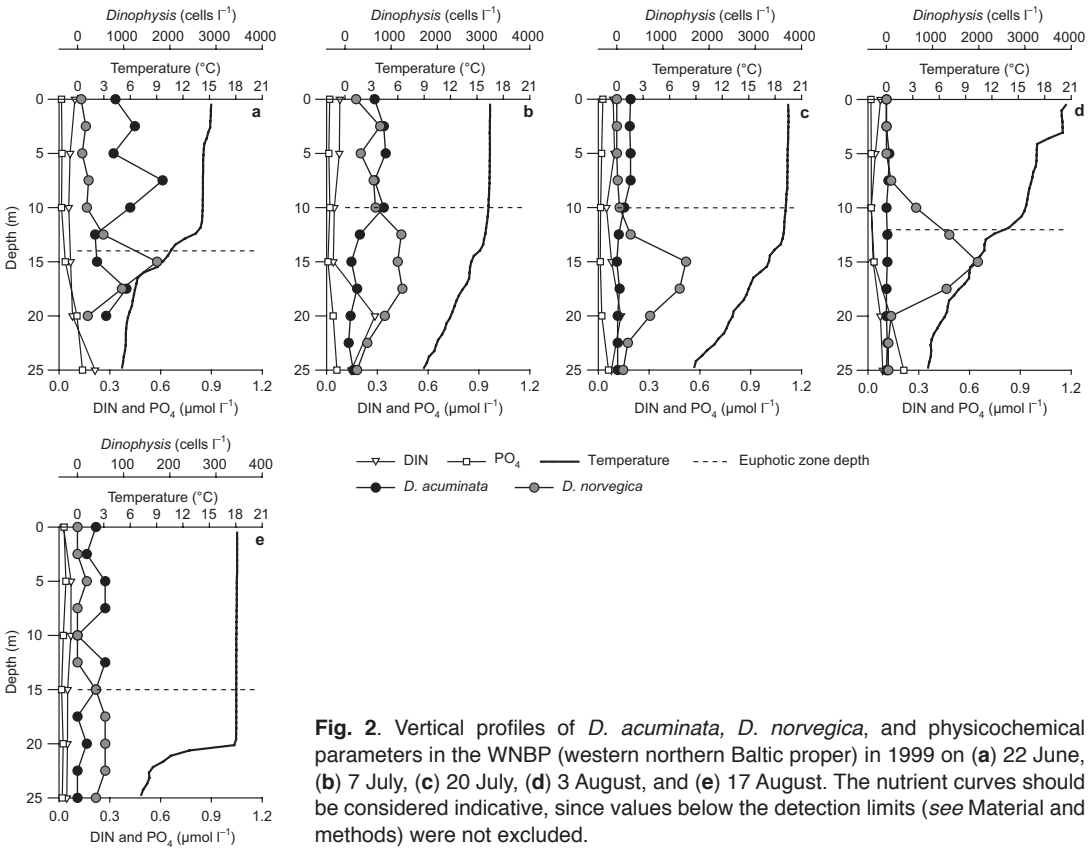

Fig. 2. Vertical profiles of *D. acuminata, D. norvegica*, and physicochemical parameters in the WNBP (western northern Baltic proper) in 1999 on (**a**) 22 June, (**b**) 7 July, (**c**) 20 July, (**d**) 3 August, and (**e**) 17 August. The nutrient curves should be considered indicative, since values below the detection limits (*see* Material and methods) were not excluded.

sites, varying in all between 6 and 15 m. In 8 out of 23 samplings the euphotic layer was at least as deep as the mixed layer (Figs. 2a, d, 3a–b, i, 4b–c, e), in all but one of the remaining cases (Fig. 3h) the thermocline was clearly (> 3 m) below the euphotic zone.

In the WNBP in 1999, the surface water temperature was > 15 °C during the whole sampling period, rising steadily to 20 °C in early August (Fig. 2a–e). The top of the thermocline (defined as the depth where the temperature decreases ≥ 1 °C m^{-1}) was found at 10–20 m. The surface water nutrient concentrations were low and increased only slightly, if at all, below 15 or 20 m, with DIN reaching 0.05–0.21 μmol l^{-1}, and PO_4 0.02–0.21 μmol l^{-1}, at 25 m. In the following year (2000, Fig. 3a–j), the surface water remained cooler, peaking at 16 °C in mid-August. The depth of the thermocline varied from 10 m to almost 30 m. Although the surface waters were again poor in nutrients, there were generally more nutrients present below 10–20 m than in 1999, with DIN reaching 0.06–0.97 μmol l^{-1} and PO_4 0.07–0.44 μmol l^{-1} at 25 m. In both years, a shallow secondary (temporary) thermocline was at times found at 3–8 m depth (Figs. 2d, 3b and f).

In the WGF in 2004 (Fig. 4a–f), the surface water temperature was low in May–June (5.5–10 °C) and higher in August (20 °C). In June, the thermocline was situated at 10–19 m and the DIN concentrations increased sharply at approximately the same depths, reaching 0.58–1.22 μmol l^{-1} at 20 m. PO_4 was more abundant at the surface and increased gradually, reaching 0.66–0.83 μmol l^{-1} at 20 m. In May and August, the water column was mixed to 30–40 m and the nutrient levels were uniform in the top 20 m layer. In May the DIN levels, and in August both the DIN and PO_4 levels, were close to or below the detection limit (Fig. 4a and f). In August a secondary thermocline occurred at 7 m (Fig. 4f).

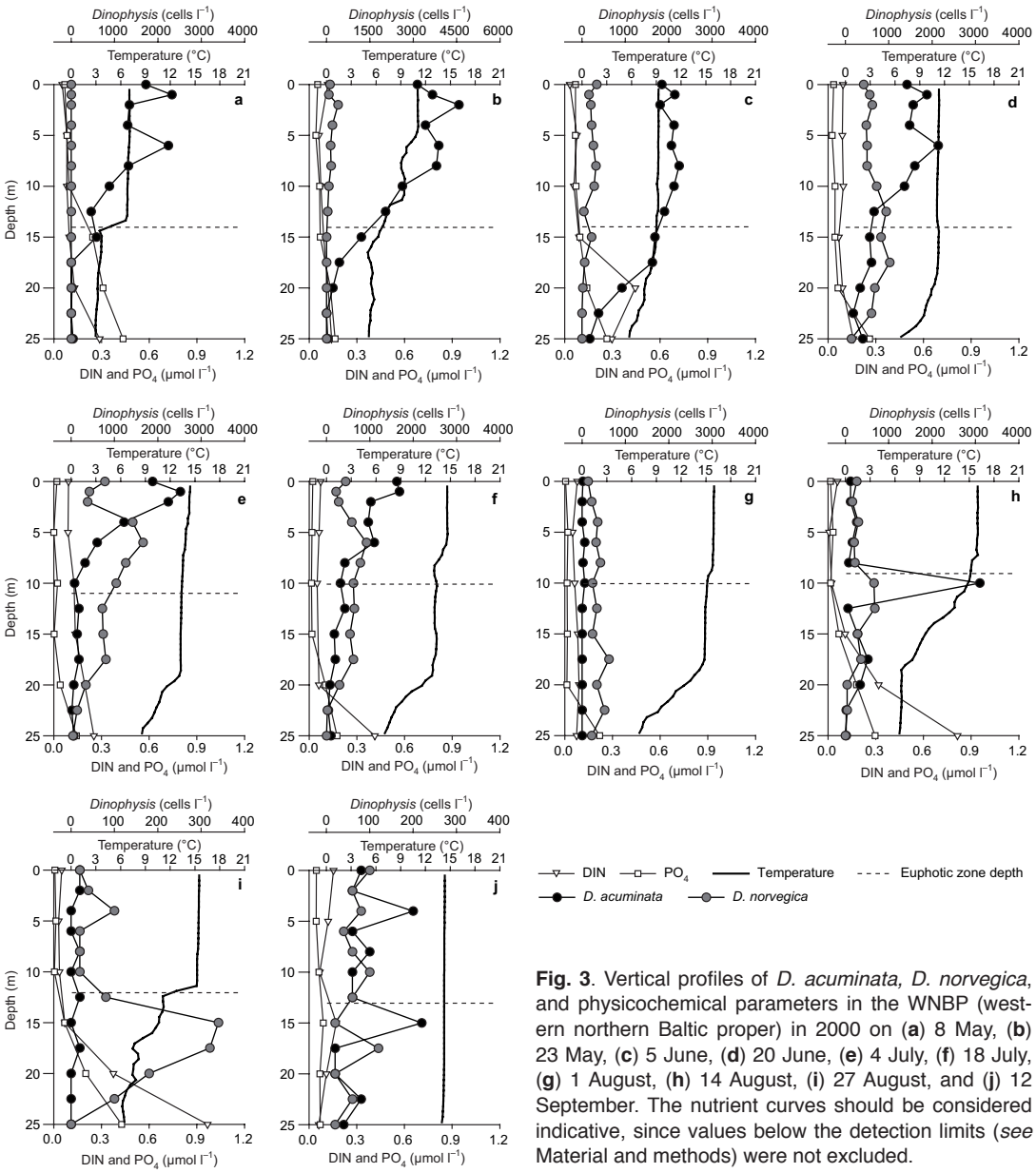

Fig. 3. Vertical profiles of *D. acuminata, D. norvegica*, and physicochemical parameters in the WNBP (western northern Baltic proper) in 2000 on (**a**) 8 May, (**b**) 23 May, (**c**) 5 June, (**d**) 20 June, (**e**) 4 July, (**f**) 18 July, (**g**) 1 August, (**h**) 14 August, (**i**) 27 August, and (**j**) 12 September. The nutrient curves should be considered indicative, since values below the detection limits (*see* Material and methods) were not excluded.

At ENBP1 and ENBP2 in July 2004 (Fig. 4g–h), the surface water temperature was ~15 °C and the thermocline was situated at 15 m and 39 m, respectively. At ENBP1, the DIN values were low except at 18 m (0.74 μmol l^{-1}), and PO_4 rose to ~0.40 μmol l^{-1} at 20 m. At ENBP2, DIN increased rapidly below 15 m to 1.14 μmol l^{-1} at 20 m, while PO_4 was below the detection limit in most of the top 20-m layer. At ENBP2, a secondary thermocline formed at 7 m (Fig. 4h).

Occurrence and abundance of *D. acuminata* and *D. norvegica*

Dinophysis acuminata occurred in high abundance (~50 million cells m^{-2}) in May, both in the WNBP (2000) and the WGF (2004) (Table 1). In August this species reached a peak abundance of ~116 million cells m^{-2} in the WGF, almost 2.5 times higher than the May values, while in the WNBP a small August peak (~11 million

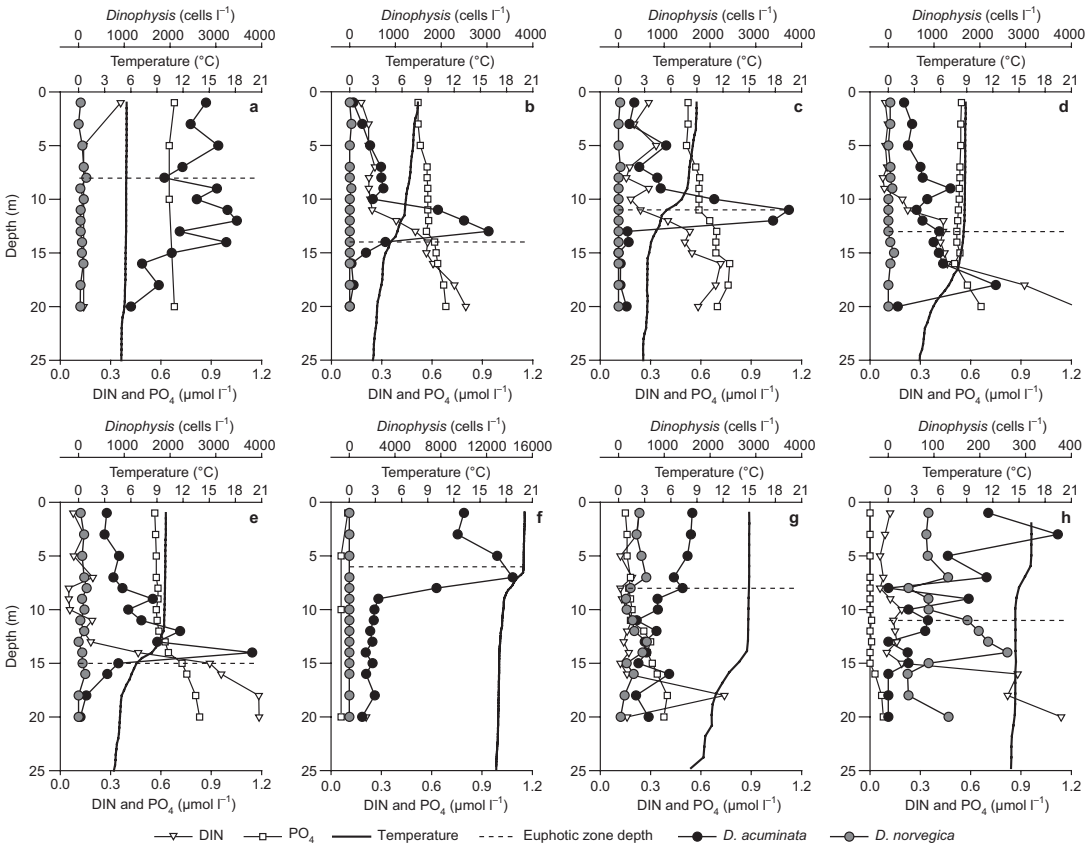

Fig. 4. Vertical profiles of *D. acuminata, D. norvegica*, and physicochemical parameters in (**a**–**f**) the WGF (western Gulf of Finland), and (**g**–**h**) the ENBP (eastern northern Baltic proper, stations ENBP1 and ENBP2) in 2004 on (**a**) 12 May, (**b**) 1 June, (**c**) 7 June, (**d**) 15 June, (**e**) 21 June, (**f**) 10 August, (**g**) 14 July, and (**h**) 19 July. The nutrient curves should be considered indicative, since values below the detection limits (*see* Material and methods) were not excluded (May and August 2004 DIN values excepted, since values below the detection limit were not available).

cells m^{-2}) appeared. In 1999, the *D. acuminata* total abundance followed much the same pattern as during the corresponding period in 2000 (except that no August peak occurred). In July 2004, *D. acuminata* occurred abundantly at ENBP1 but sparsely at ENBP2 (~20 million and 2 million cells m^{-2}, respectively).

Dinophysis norvegica occurred most abundantly in the WNBP during late June to early or mid-August, with maxima of ~16 million and ~18 million cells m^{-2} in early July 1999 and 2000, respectively. In July 2004, it was moderately abundant (~7 million cells m^{-2}) at ENBP1. At all other times in the WNBP, as well as in the WGF and at ENBP2, the species occurred only in low amounts (< 4 million cells m^{-2}), if at all.

Vertical distribution of *D. acuminata* and *D. norvegica*

In general, *D. acuminata* and *D. norvegica* formed population maxima either (1) in the mixed and usually illuminated surface waters above 10 m depth, or (2) below 10 m depth, in or out of the euphotic zone but near the thermocline, coinciding with a nutricline. Vertical profiles with maximum cell densities < 250 cells l^{-1} (Table 1) were not considered, due to the low precision (large confidence limits) of the results when only a few cells were counted. Five of the *D. acuminata* (Figs. 2d–e, 3g, i–j) and almost half of the *D. norvegica* (Figs. 2e, 3a, j, 4a–f) observations were thus excluded. Although the

time of sampling varied from late morning to early afternoon, all samplings were done during the daylight hours, and at least no effect of diel vertical migration was observed.

Most of the *D. acuminata* population was usually found in the mixed surface layer (cell density maxima 300–4600 cells l^{-1}, Figs. 2a–c, 3a–f, 4f–h). The species was particularly abundant (> 7600 cells l^{-1}) down to 8 m depth with a pronounced maximum of 14 300 cells l^{-1} at 7 m in the WGF in August 2004 (Fig. 4f). Subsurface maxima of *D. acuminata* were primarily formed in the WGF, once also in the WNBP (Figs. 3h, 4b–e). These occurrences usually had a very well-defined peak of 2300–3800 cells l^{-1} at the depth of 10–18 m.

Dinophysis norvegica predominantly formed subsurface maxima. These occurred at the depths between 10 and 17.5 m in the WNBP in June–August and at ENBP2 in July (Figs. 2a–d, 3d, g–i, 4h). Due to lower cell densities (300–2000 cells l^{-1}), these subsurface maxima were seldom as distinct as those of *D. acuminata*. Only in the WNBP in 2000 did the bulk of the *D. norvegica* population occur in the mixed surface layer (Fig. 3b–c, e–f). The highest cell densities on these occasions were low to moderate (300–900 cells l^{-1}) and the profiles lacked pronounced maxima. The *D. norvegica* surface layer peak was conspicuous (1700 cells l^{-1}) only in early July, and although both *D. norvegica* and *D. acuminata* formed surface layer maxima, depth segregation between them was observed (Fig. 3e).

Table 1. Integrated total abundances (10^6 cells m^{-2}; 0–20 m) and maximum cell densities (cells l^{-1}; 0–25 m in the WNPB, 0–20 m in the WGF and ENBP) of *D. acuminata* and *D. norvegica*.

Site/Date		*D. acuminata*		*D. norvegica*	
		Integr.	Max.	Integr.	Max.
WNBP	22 June 1999	18.95	1800	10.28	1700
	7 July 1999	10.75	900	16.33	1200
	20 July 1999	3.25	300	9.00	1500
	3 Aug. 1999	0.35	< 100	13.58	2000
	17 Aug. 1999	0.68	< 100	0.38	< 100
WNBP	8 May 2000	19.52	2300	0	0
	23 May 2000	49.67	4600	2.02	400
	5 June 2000	37.52	2200	3.69	300
	20 June 2000	23.41	2100	14.08	1000
	4 July 2000	12.61	2500	18.48	1700
	18 July 2000	11.80	1700	11.69	900
	1 Aug. 2000	0.32	< 100	6.75	600
	14 Aug. 2000	10.91	3100	6.86	700
	27 Aug. 2000	0.20	< 100	2.56	300
	12 Sep. 2000	1.83	200	1.33	100
WGF	12 May 2004	48.35	3500	1.30	200
	1 June 2004	13.35	3000	0.11	< 100
	7 June 2004	15.61	3700	0.13	< 100
	15 June 2004	17.84	2300	0.60	100
	21 June 2004	20.22	3800	1.60	200
	10 Aug. 2004	115.78	14300	0	0
ENBP1	14 July 2004	20.21	1600	6.96	600
ENBP2	19 July 2004	2.23	400	2.15	300

Discussion

Occurrence and abundance

In the WNBP, *D. acuminata* integrated total abundances culminated in May–June, which is in agreement with previous reports from the area (Hobro 1979, Hajdu 2002, Hajdu and Larsson 2006). In the WGF, *D. acuminata* maximum occurrences are less predictable and its main occurrence varies from early summer to autumn (Kononen and Niemi 1984, 1986, Tamelander 2000); accordingly we observed abundance peaks in both May and August. In the Baltic Sea, this species commonly occurs in densities from less than 100 to a few thousand cells l^{-1}, and to the best of our knowledge the peak value of 14 300 cells l^{-1} we observed in August 2004 is among the highest reported from the Gulf of Finland.

The *D. acuminata* peak observed in the WNBP in August 2000 was small but distinct (Fig. 3h and Table 1) and consisted mainly of small-sized, senescent cells at 10 m. The species occurred very sparsely in both the previous and the following samplings, and since the cells were already deteriorating and many empty thecae were observed, the population may have been brought to the area through advection or upwelling. Hydrodynamic events are known to cause rapid fluctuations in *D. acuminata* cell densities (e.g. Godhe *et al.* 2002). Hydrodynamics may also have played an indirect role in the *D. acuminata* proliferation in the WGF in August 2004 (Fig. 4f), which coincided with a *Heterocapsa triquetra* bloom (data not shown). Although both DIN and PO_4 were depleted to 20 m depth at the time of our sampling, strong winds

earlier that month deepened the mixed layer to 35–40 m (Kuuppo *et al*. 2006) and may have supplied the surface waters with nutrients that fuelled the growth of *D. acuminata* and *H. triquetra*.

Dinophysis acuminata was present at every sampling, and we found it in abundance at temperatures between 5.5 and 20 °C, which attests to the versatility of this species. Worldwide, it occurs at temperatures from almost freezing (in ice samples, e.g. Huttunen and Niemi 1986) up to 29.4 °C (Nishitani *et al*. 2002). Elevated densities usually occur in a narrower range, but Marshall *et al*. (2004) found high abundances (from thousands of cells l^{-1} up to 236 000 cells l^{-1}) at 4.4–20.7 °C, a temperature range that corresponds well with our results. This species has been recorded in salinities from 3.8 (Wasmund *et al*. 1999) to 37 (Madigan *et al*. 2006) and, again, it often tolerates a wide range within an area (Nishitani *et al*. 2002, Marshall *et al*. 2004). Within the narrow salinity range of the present study (5.5–6.9 in the top 20–25 m), preferences were neither expected nor observed.

Where *D. acuminata* and *D. norvegica* co-occur, they often peak at different times (Séchet *et al*. 1990, Maranda 1995, Hajdu 2002). In the WNBP, *D. norvegica* reached its maximum about one month later than *D. acuminata*, in accordance with previous results (Hajdu 2002). *Dinophysis norvegica* was less abundant than *D. acuminata*, expressed as both integrated total abundances and maximum cell densities. Also in the WGF, the overall abundance of *D. acuminata* clearly surpasses that of the sparsely occurring *D. norvegica*, based on our results and those of Kuuppo *et al*. (2006). The seasonal development observed in this region earlier (Tamelander 2000) suggests that we and also Kuuppo *et al*. (2006) may have missed the highest abundances of *D. norvegica*, since there are no data from the WGF in late June–late July. In the mid-July samples from the ENBP the same year, only low to moderate *D. norvegica* abundances were present, and we may have missed the peak, if such occurred, also in this area. The overall dominance of *D. acuminata* over *D. norvegica* in the northern Baltic Sea lends support to previous results (Hajdu 2002).

The lack or low abundances of *D. norvegica* can in most cases be explained by the prevailing temperature and/or salinity conditions. Our data show that in comparison to *D. acuminata*, *D. norvegica* displays an inferior tolerance to both low and high temperatures as well as low salinity, thus being nearer its marine origins than *D. acuminata*. In the WNBP, we found *D. norvegica* only after surface temperatures had risen to 9 °C and in greater number only after the temperature at the depths where *D. norvegica* presided rose to around 11 °C. Furthermore, the highest numbers (> 1000 cells l^{-1}) were always at salinities of around 6.5. In the WGF, where *D. norvegica* cell densities even at best were < 200 cells l^{-1}, surface water temperatures did not reach 10 °C until late June, and in mid-August the water temperature was 17–20 °C throughout the upper 20-m layer. Moreover, salinity was well below 6 in May and August.

The above conclusion of restrictive temperature and/or salinity conditions is supported by previous findings. Although *D. norvegica* was also found in sea ice (Ikävalko 2004), Hajdu (2002) observed that this species requires at least temperatures of > 8–9 °C to increase in numbers in the northern Baltic Sea. At the other end of the temperature scale, in the central Baltic Sea *D. norvegica* was found most abundantly at depths of 5–18 °C, preferring these layers to surface waters of ca. 15 to > 20 °C (Carpenter *et al*. 1995, Gisselson *et al*. 2002, Hajdu *et al*. 2002: figs. 3b and 13). In light of the above, the suggestion that successive upwellings promote abundant occurrences of *D. norvegica* in the WGF (Kononen and Niemi 1986) is a reasonable proposition, since upwelling causes a drop of several degrees in surface temperature and an increase in salinity (Haapala 1994). Although the species has been found at salinities as low as 4.8 (Niemi 1971), Hajdu (2002) noted that in the northern Baltic Sea it apparently requires a salinity of > 6. Heiskanen *et al*. (2005) also suggested that *D. norvegica* may be restricted by low salinity in the northern Baltic Sea. However, true physiological studies of *D. norvegica* from the Baltic Sea (and elsewhere) are lacking.

Vertical distribution

When *D. acuminata* and *D. norvegica* co-occurred, their abundances peaked at different

depths (Figs. 2a–c, 3d–f, 4h). Consequently, each species 'behaved' as they did when investigated separately in the Baltic Sea, i.e. *D. acuminata* mainly occupied the top ca. 10 m of the mixed layer (Figs. 2a–c, 3a–f, 4f–h; cf. Balode and Purina 1996, Olli 1999, Kuuppo *et al.* 2006), while *D. norvegica* typically resided in the thermocline region at ca. 10–20 m depth (Figs. 2a–d, 3d, g–i, 4h; cf. Carpenter *et al.* 1995, Gisselson *et al.* 2002, Hajdu *et al.* 2007). Less expected were the observations of *D. acuminata* at the seasonal thermocline (Figs. 3h, 4b–e; but also reported by Kuosa 1990, Balode and Purina 1996), and of *D. norvegica* in the upper ca. 10 m of the mixed layer (Fig. 3b–c, e–f), where peaks have only infrequently been observed (Gisselson *et al.* 2002).

Nutrition

In all cases when *D. acuminata* and *D. norvegica* formed surface layer maxima, the surface waters were depleted of inorganic nutrients. While remaining in the euphotic zone would facilitate photosynthesis, low nutrient levels raise the question of resource availability. The relationships between inorganic nutrient concentrations and the occurrence of *D. acuminata* and *D. norvegica* have repeatedly been considered (e.g. Subba Rao *et al.* 1993, Johansson *et al.* 1996, Godhe *et al.* 2002), but correlations have been difficult to establish. A valid possibility may be the rapid remineralisation and recycling of inorganic nutrients, but the rate and quantity of this regeneration are difficult to measure.

A solution to inorganic nutrient limitation is supplementing photosynthesis with the uptake of organic matter, i.e. utilising mixotrophy. The utilisation of dissolved organic matter (DOM) is yet to be demonstrated for *D. acuminata* (however, *see* Lunven *et al.* 2005, Velo-Suarez *et al.* 2008) and *D. norvegica*, but it has been shown for other dinoflagellates (reviewed by Carlsson and Granéli 1998). Moreover, several studies have shown that *D. acuminata* and *D. norvegica* ingest particulate organic matter (POM; e.g. Jacobson and Andersen 1994, Carvalho *et al.* 2008 and references therein), and Park *et al.* (2006) succeeded in culturing *D. acuminata* by providing the ciliate *Mesodinium rubrum* (*Myrionecta rubra*) as food. It has not been verified whether *D. acuminata* (or *D. norvegica*) preys on *M. rubrum* in the Baltic Sea. Short-term diel vertical distributions do not elucidate the potential prey-predator relationship between these species (cf. Olli 1999, Hajdu *et al.* 2007).

Growth on POM and/or DOM would explain the high *D. acuminata* abundance in early summer; after the spring bloom had depleted the surface water of nutrients, it was still likely rich in organic matter. The August 2004 proliferation of *D. acuminata* was presumably generated by nutrient input from deeper waters, but organic matter from the coincident *H. triquetra* bloom could have contributed. Elevated densities of *D. acuminata* have previously been observed following phytoplankton blooms elsewhere (e.g. Lassus *et al.* 1985, Dahl and Johannessen 2001).

Dinophysis norvegica is considered to be mainly heterotrophic in the Baltic Sea because it typically resides at the thermocline, where usually < 5% and often only < 1% of noontime surface irradiance remains (Gisselson *et al.* 2002, *see* also Hajdu *et al.* 2007). Likewise, in the present study all distinct *D. norvegica* subsurface peaks (Figs. 2a–d, 3h–i, 4h), while occurring in the thermocline (secondary thermocline at ENBP2) and coinciding with a slight DIN and/or PO_4 increase, were positioned below the euphotic zone. In previous studies in which *D. norvegica* was found under similar circumstances, the investigators concluded that *D. norvegica* was primarily heterotrophic, since virtually no net photosynthesis took place (Carpenter *et al.* 1995), photosynthesis could not have sustained the growth rates observed (Gisselson *et al.* 2002) and no evidence of diel vertical migration was found. This observed lack of migration (Carpenter *et al.* 1995) or only very limited migration (Hajdu *et al.* 2007) may be an accurate observation, but it may also be an artefact caused by sampling strategies inadequate for detecting (non-diel) migration patterns. Prolonged, non-diel vertical migration has been observed for other dinoflagellates (Kononen *et al.* 2003 and references therein) and convincingly proposed for *D. acuminata* (Setälä *et al.* 2005). Thus, the conclusion of heterotrophy as the primary nutritional mode of *D. norvegica* in subsurface

peaks is plausible, but not fully indisputable; it is possible that the population is in fact performing non-diel nutrient retrieval migration.

Our observation that *D. norvegica* forms surface layer maxima presents the possibility that it may utilise photoautotrophic nutrition to a greater extent than lately suggested, based on investigations of thermocline maxima (Carpenter *et al.* 1995, Gisselson *et al.* 2002, Carvalho *et al.* 2008). We ask, why would an organism have pigments (particularly if they are kleptochloroplasts, cf. Janson 2004, Carvalho *et al.* 2008, Minnhagen *et al.* 2008), that take up cellular space that could be used for food vacuoles and that furthermore make the organism more easily spotted by predators, if not to use them at all? Unfortunately, we have no data on photosynthetic rates or incorporation of organic matter either to validate or dispute the utilisation of photoautotrophy. It is, however, corroborated by the results of Mouritsen and Richardson (2003), who found that the vertical microscale distribution patterns of autotrophic and heterotrophic dinoflagellates differ significantly. While mixotrophs occurred in both groups, *D. acuminata* and *D. norvegica* grouped with the autotrophs (Mouritsen and Richardson 2003).

In contrast to *D. norvegica*, *D. acuminata* appeared to avoid darkness when forming subsurface maxima. These peaks coincided with the thermocline and a distinct nutricline and usually occurred within the illuminated layer. Conversely, in the WNBP where the spring bloom depleted nutrients from far deeper than the euphotic zone, *D. acuminata* was not associated with the thermocline. Here, daytime aggregation at the nutricline would have meant a position in darkness and *D. acuminata* apparently preferred the illuminated but nutrient-depleted surface layer. This dependency on light is supported by recent experiments by Kim *et al.* (2008) and Riisgaard and Hansen (2009) on cultured *D. acuminata*. Based on their results, Riisgaard and Hansen (2009) suggested that *D. acuminata* may often be prey-limited in its natural environment and that therefore photosynthesis, which at low prey densities is responsible for most of the carbon uptake, may be the primary carbon source in nature. Furthermore, Kim *et al.* (2008) found that *D. acuminata* failed to grow in darkness, even when *M. rubrum* was provided as prey, while Riisgaard and Hansen (2009) discovered that under illuminated conditions *D. acuminata* remained growing for at least 10–14 days, even though no prey was provided.

Water column stability

All distinct *D. norvegica* subsurface maxima coincided with a shallow mixed layer (down to 7–13.5 m), indicating that stratification, particularly at a relatively shallow depth, is important in promoting *D. norvegica* subsurface populations. This is corroborated by previous investigations (Subba Rao *et al.* 1993, Gisselson *et al.* 2002). In contrast to the warm and sunny summer of 1999, the following summer (July in particular) was extremely rainy, unstable and somewhat cooler than usual (SMHI 1999, 2000). Consequently, the mixed layer was deep (18–23 m) during the 2000 *D. norvegica* peak season (Fig. 3d–g). We found that although this did not affect *D. norvegica* abundance (Table 1), the species did not sustain subsurface maxima, but instead formed indistinct subsurface occurrences or remained in the surface layer. Turbulent disruption of the subsurface population has been put forward as the cause for *D. norvegica* occupying the surface layer (Gisselson *et al.* 2002). However, simultaneously with a surface layer occurrence (Fig. 3f), we observed a secondary (temporary) thermocline which indicates that low mixing conditions had prevailed for some time.

Carpenter *et al.* (1995) suggested that the *D. norvegica* preference for deeper layers may be an avoidance of warm surface waters. A common denominator for the *D. norvegica* thermocline occurrences in our study was, in fact, warm surface water temperature (15–20.5 °C, compared with < 10–17 °C at *D. norvegica* maxima). Furthermore, in 2000 when the surface water was cool (≤ 16 °C), *D. norvegica* did not form as distinct subsurface maxima. Thus, in addition to physically disrupting a subsurface population, mixing likely lowers the surface water temperature and increases surface salinity, ostensibly rendering the surface layer environment more suitable for this species, as suggested above for upwelling effects.

Dinophysis acuminata, while frequently associated with thermal and/or salinity stratification (Peperzak *et al*. 1996, Reguera *et al*. 2003, Lindahl *et al*. 2007), also occurs in relatively well mixed waters (Maranda 1995, this study Fig. 4a). Like *D. norvegica*, also this species formed an indistinct subsurface maximum in a deep mixed layer (Fig. 4d). However, in general most of the *D. acuminata* population was found in the upper 10 m, irrespective of thermocline depth. These surface layer maxima were generally less pronounced than the subsurface peaks, probably due to the lack of steep clines in the surface layer. It is reasonable to presume that low turbulence makes it easier for both species to maintain a preferred position, both in the surface and subsurface layers. However, stratification and the depth of the mixed layer seem to be more important for *D. norvegica*.

The shallow, apparently warm and windless weather conditions induced, secondary (temporary) thermoclines that were present on five occasions (Figs. 2d, 3b, f, 4f, h), did not influence the vertical distribution of *D. acuminata* and *D. norvegica* in a consistent way, since the populations were found above, at, or below them. This shows that either the temperature differences above and below the clines are too small to affect *Dinophysis* distribution, or there is a factor overruling the apparent stability of the surface layer (e.g. nutrients, salinity, light, food).

In all, the vertical positioning of the *Dinophysis* populations can be summarised as follows:

1. Surface layer maxima of both *D. acuminata* and *D. norvegica* occurred within the illuminated but nutrient-poor mixed layer. While most of the *D. acuminata* population was found in the top 10 m irrespective of temperature or thermocline depth, only a combination of cool surface waters and a relatively deep mixed layer drew *D. norvegica* closer to the surface. Active growth of these populations seemingly requires rapid recycling of nutrients, and/or nutrient retrieval migration to facilitate photosynthesis, and/or the utilisation of a heterotrophic diet.
2. *Dinophysis acuminata* subsurface maxima were found within the illuminated layer, at the thermocline, and were related to sharper nutriclines than those of *D. norvegica*. The conditions prevailing at the *D. acuminata* subsurface maxima appear to facilitate photosynthetic growth, but do not exclude a combined, i.e. mixotrophic, diet. When the spring bloom consumed nutrients from water layers far deeper than the euphotic layer, *D. acuminata* did not seek out the thermocline region. *Dinophysis acuminata* thus appears to be sensitive to low light.
3. All distinct *D. norvegica* subsurface peaks occurred in the thermocline, usually coincided with a rather modest increase in DIN and/or PO_4, and were positioned below the euphotic zone. Thus, this species does not seem as sensitive to low light. In a deep mixed layer, *D. norvegica* did not form well-defined subsurface maxima, indicating that the thermocline peaks are promoted by stratification at a fairly shallow depth. Active growth of *D. norvegica* thermocline populations would seemingly require the utilisation of either heterotrophy or, from the perspective of these populations, a 'light retrieval' migration, or a combination of both.

Conclusions

Dinophysis research is known to be plagued by ambiguous and inconsistent results and few easy answers. In compliance with this tradition, our results agree with some previous findings while questioning others.

We found that the abundance maxima of *D. acuminata* and *D. norvegica* were segregated both seasonally and vertically and conclude that these species undertake differing survival strategies in the northern Baltic Sea. *Dinophysis acuminata* occurred in elevated abundances early and late in the summer, during or after periods of high phytoplankton biomass, while *D. norvegica* was abundant during a shorter period, peaking one month after the first *D. acuminata* maximum. The salinity- and temperature-tolerant *D. acuminata* is the more successful species and our results expand the wide range of scenarios in which it may bloom worldwide. *Dinophysis norvegica* is probably restricted by both low salinity and low and high temperatures in the northern Baltic Sea.

Both *D. acuminata* and *D. norvegica* principally formed population maxima either in the mixed surface waters or near the thermocline. *Dinophysis acuminata* was usually found in the surface layer, but in the presence of light and a distinct nutricline it formed pronounced subsurface peaks. *Dinophysis norvegica*, on the other hand, predominantly formed thermocline maxima, and was not as sensitive to low light. However, when rainy and cool weather conditions prevailed during the *D. norvegica* peak season, the species did not sustain clear subsurface maxima but instead formed indistinct subsurface occurrences or remained in the mixed surface layer. When *D. acuminata* and *D. norvegica* co-occurred, their abundances peaked at different depths; this was observed even when both species formed maxima in the surface layer.

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